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The Domain of the Replicators

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CA☆ FORUM ON THEORY IN ANTHROPOLOGY

The Domain of the Replicators

Selection, Neutrality, and Cultural Evolution

by J. Stephen Lansing and Murray P. Cox

Do cultural phenomena undergo evolutionary change, in a Darwinian sense? If so, is evolutionary game theory (EGT) the best way to study them? Opinion on these questions is sharply divided. Proponents of EGT argue that it offers a unified theoretical framework for the social sciences, while critics even deny that Darwinian models are appropriately applied to culture. To evaluate these claims, we examine three facets of cultural evolution: (i) cultural traits that evolve by Darwinian selection, (ii) cultural traits that affect biological fitness, and (iii) coevolution of culture and biology, where selection in one affects evolutionary outcomes in the other. For each of these cases, the relevance of EGT depends on whether its assumptions are met. Those assumptions are quite restrictive: selection is constant, time horizons are deep, the external environment is not part of the game, and neutral processes such as drift are irrelevant. If these conditions are not met, other evolutionary models such as neutrality, coalescence theory, or niche construction may prove more appropriate. We conclude that Darwinian processes can occur in all three types of cultural or biological change. However, exclusive reliance on EGT can obscure the respective roles of selective and neutral processes.

In a series of three lectures given in honor of Stanisław Ulam at the Santa Fe Institute in the fall of 2003, Harvard biologist Richard Lewontin offered cogent reasons why the application of Darwinian evolutionary models to culture is a dead end. There is no question, he argued, that culture exists in humans; one can argue whether it is possessed by higher apes, but it is certainly not present in jellyfish. But models of cultural change inspired by Darwinian processes begin with a false premise because this population model of variation, inheritance, and differential rates of reproduction was specifically designed to explain a particular set of natural phenomena that have a well-known empirical and mechanistic base. Cultural evolutionists have no set of phenomena of comparable concreteness; they cannot even reach agreement on how to define and describe their objects of interest.

Yet interest in cultural evolution is increasing. As Kevin

Laland pointed out at a conference at Durham University in 2007, a quick check of Web of Science shows that publications and keywords associated with cultural evolution are in a period of rapid growth. In 2003, the year Lewontin gave his skeptical lectures in Santa Fe, Harvard launched a new program in evolutionary dynamics. The program's director, Martin Nowak, described evolutionary game theory as poised to unite the study of adaptive agents of all kinds, from genes and viruses, to cultures and languages:

The applications of evolutionary game theory pervade by now all areas of biology. Interactions among genes, viruses, cells, and humans are often instances of evolutionary games that are amenable to empirical and theoretical investigation. Game theory is the appropriate tool whenever the success of an individual depends on others. (Nowak and Sigmund 2004:798)

Among contemporary cultural evolutionists, this view has rapidly gained adherents. Evolutionary game theory is seen as offering a powerful new foundation for studies of cultural and behavioral evolution, one that promises to bond the social sciences together under a unified theoretical framework (Gintis 2006; Mesoudi, Whiten, and Laland 2006).

The mathematical foundation of evolutionary game theory is the "the replicator equation" (Hofbauer and Sigmund 1988: 147; Nowak 2006:3, 56). This equation is an optimization

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method that captures the essence of the Darwinian process of selection, given certain simplifying assumptions. It has been very successfully used to characterize frequency-dependent selection and thereby gain insights into the evolution of behavior. But like all mathematical formalizations, the method's utility ultimately depends on the nature of the question. In contemporary biology, the replicator equation is just one of many tools used to investigate evolutionary processes. This was not always the case: as late as the 1960s, the prevalent view held that almost all mutations are under selection, but subsequent discoveries in molecular biology led to a reappraisal of the role of selection in evolutionary change. Today, geneticists do not assume that most genetic changes are caused by selection—an underlying premise in evolutionary game theory. Instead, selection is inferred only when a null model of neutrality can be rejected (Gould 1989). A similar debate around the role of selection is now taking place in theoretical ecology (Alonso, Etienne, and McKane 2006; Hubbell 2001), and recently a few anthropologists have also begun to develop techniques to distinguish selection from neutral processes in cultural phenomena (Bentley, Hahn, and Shennan 2004; Lansing et al. 2008; Neiman 1995; Shennan and Wilkinson 2001; the question was posed earlier by Cavalli-Sforza and Feldman 1973, 1981).

In the first section of this paper, we review the history of cultural evolution in light of Lewontin's challenge. Are there cultural phenomena that undergo evolutionary change, in a Darwinian sense? If so, is it appropriate to assume that these systems are undergoing selection and are thus suited to modeling as evolutionary games?¹ Alternately, do neutral processes also play a role? We pursue these questions across a range of examples, from the naming of American children to male dominance in Indonesian villages. Next, we consider the significance of the environment for cultural evolution. The external biophysical environment has no role in evolutionary games, but other kinds of evolutionary models can be used to incorporate interaction between behavior and environment. Given these alternative approaches, we suggest that the usefulness of replicator models depends on the answers to three questions: Does the system under investigation fit a Darwinian model of heritable variation? Is there evidence that evolutionary selection has occurred? Is this selection process uncoupled from the external environment?

When the answer to all three questions is affirmative, then the replicator models of evolutionary game theory may offer

1. Selection operates whenever individuals reproduce at different rates. It can, of course, take many forms: directional, balancing, or frequency dependent. Frequency-dependent selection is a common focus of many evolutionary games, that is, wherever changes in the frequency of one group of players affect the frequency of the others. Nevertheless, in evolutionary games, the environment consists solely of these other agents. A key point we address here is the inability of game theory to model different forms of environmental feedback; the environment, we claim, is often more than just the sum of the other players in the game.

insights into cultural evolution. But how often are these conditions met?

Selection and the Neutral Theory

In biology, the assumption that phenotypic variation is entirely the result of selection began to be questioned in the 1960s as molecular biology started to obtain empirical data that could be compared to the mathematical predictions of population genetics. In 1968, geneticist Motoo Kimura predicted that the vast majority of evolutionary changes at the molecular level are caused not by selection but by random drift of selectively neutral mutants. Even in the absence of selection, Kimura reasoned, evolutionary change will occur as a result of chance, and this could be analyzed with tools from probability theory. The idea that selection might have little, or no, role in shaping portions of the genome was not altogether new: Sewall Wright emphasized the importance of neutral processes such as drift as early as the 1930s (Provine 1989). But Kimura took this idea further, offering a probabilistic method for the detection of selective effects that could be readily tested with data from the genome.

In genetics, the neutral theory was hotly debated for decades. As Kimura observed in his 1968 paper, the prevalent view in the 1960s held that almost all mutations are under selection, and this opinion was slow to change. But as Stephen J. Gould wrote in 1989, "These equations give us for the first time a baseline criterion for assessing *any kind* of genetic change. If neutralism holds, then actual outcomes will fit the equations. If selection predominates, then results will depart from [neutral] predictions" (Gould 1989:16). Kimura's work eventually led to a dramatic reversal in the way selection is viewed in molecular biology: geneticists now infer selection only when it can be shown that the assumption of neutrality has been violated. The success of the neutral theory triggered a shift in perspective, from the fitness of individual units of selection, to the population-level consequences of both drift and selection.

But is the neutral theory relevant above the molecular level? Theoretical ecologists began to consider this question in the 1990s. Previously, the prevalence of species in ecological communities was approached from a pan-selectionist perspective: what are the special attributes of each species that explain its abundance in a given environment? The neutral theory offered an alternative hypothesis. If one assumes that species do not differ in their competitive abilities, what would their prevalence be if it depended only on the total size of the ecological community and the chance arrival of new species? In other words, what role do neutral processes play in the formation and persistence of ecological communities? This question is now perhaps the most hotly debated topic in theoretical ecology (Alonso, Etienne, and McKane 2006; Harte 2003). Mathematically, the neutral theory in ecology is faithful to its origins in genetics; both rely on the same underlying

mathematical model. Although the scope of the neutral theory in ecology is still being tested, a shift is clearly under way from the assumption of pan-selectionism to the view that selection can only be inferred by showing departure from a null model of neutrality (Hey 1999; Hu, He, and Hubbell 2006; Leigh 2007).² As in genetics, this represents a change in the level of analysis, from the fitness of individuals to the effects of selection at the community level.³ As Kimura wrote in 1983, "It is easy to invent a selectionist explanation for almost any specific observation; proving it is another story. Such facile explanatory excesses can be avoided by being more quantitative" (Kimura 1983:xiv).

Cultural Evolution

So when, if ever, is cultural change an evolutionary process? And can neutral tests even be applied to them? Broadly speaking, these ideas are not new (Cavalli-Sforza and Feldman 1973, 1981), but they are not exactly coffee table subjects within anthropology today. To frame our discussion, we begin by asking what is meant by cultural evolution in a Darwinian context. We consider three quite different versions of this idea in contemporary anthropology:

Type 1: purely cultural evolution. Culture is a domain apart from biology, but it evolves in the same way. For this to be true, cultural phenomena must comprise populations of elements that have differential reproductive success based on attributes that are both heritable and subject to selection. Richard Dawkins's "memes" are examples; so too are the (mathematical) strategies that evolve in evolutionary games. (For a critical review, see Ehrlich and Feldman 2003.)

Type 2: culture as it affects biological evolution. In this interpretation, cultural evolution is the heritable nongenetic transmission of any trait that affects the reproductive success of individuals (Heyer, Sibert, and Austerlitz 2005). The increased prevalence of deleterious genetic disorders in the Ashkenazi is an example of this evolutionary process.

Type 3: gene-culture coevolution. Darwinian processes occur in both culture and biology. They can interact, producing a coevolutionary dynamic (Durham 1991; McElreath and Henrich 2007), such as the coupled evolution of cattle farming and adult lactose tolerance.

2. As Leigh observes (2007:2076), "no population geneticist, not even Kimura, sought to deny the importance of adaptive evolution. Instead, all major workers were interested, at least to some degree, in how neutral processes affected adaptive evolution." In ecology, as Leigh further notes (p. 2087), everyone, even the advocates of the neutral theory, recognizes that neutral theory is wrong when taken to extremes: adaptive processes clearly do matter. In genetics, the question of precisely which regions of the genome are under selection is being revisited using neutral theory (see Hey 1999). What is common to both genetics and ecology (and, we might add, to anthropology) is the option of using neutrality as a null theory.

3. In genetics, the neutral theory refers to populations of individuals, while in ecology, it refers to the species composition of ecological communities (i.e., species are the "individuals").

We begin with type 1 cultural evolution and ask whether it is possible to apply a version of the neutral theory to cultural phenomena and thus distinguish between the effects of selection and drift. Hahn and Bentley (2003) investigated this question when they examined the changing frequencies of baby names in the United States. One can easily imagine a selectionist explanation for the prevalence of names within a society; for example, in each generation parents might preferentially choose the names of culturally dominant or prestigious individuals for their children. The alternative, neutral hypothesis would predict a distribution of names that appears no different from that produced solely by chance.⁴ In 2002, the Social Security Administration published the thousand most common baby names in each decade of the twentieth century, based on a sample of 5% of all social security cards issued to Americans. Most parents chose a preexisting name for their infant, but occasionally a new name was introduced. Hahn and Bentley found that a very few names were extremely popular, while others persisted at lower frequencies.

To discover whether the popularity of names is caused by selection or neutral drift, the researchers created a simulation based on Kimura's neutral theory and compared their results with the observed data. With the reader's indulgence, the processes that lead to neutral equilibrium can be explained with the statistician's favorite example, a bag of colored marbles. To model the effects of drift, the experimenter reaches into the bag and grabs two marbles. One is randomly tossed aside, while the other is magically duplicated; the latter (now identical) pair of marbles is put back into the bag. Starting with a bag of 10 marbles, each with a different color, all the marbles in the bag will have the same color after only a few replacements. This process will take much longer with bags of 100 or 1,000 marbles.

Thus, drift reduces the number of colors in the bag. Mimicking the effects of mutation can counteract this process: from time to time a marble with a new color is added to the bag as replacement for a discarded marble. Neutral equilibrium is reached when the introduction of new colored marbles by mutation matches the rate at which existing colors are

4. This usage raises an important semantic point, the meaning of terms such as "selection," "random," and "chance." In an evolutionary sense, these words have very specific meanings that may differ from common usage—for instance, they are frequently used as descriptors of change at the population level. Consider: at some point, individuals will usually choose a life partner; a choice that is generally considered highly selective and distinctly nonrandom. But mate choice may not differ from expectations under a model of random choice when considered at larger scales, such as the perspective of an entire population. Many of the Indonesian communities discussed later do not reject neutrality, which implies that they are also probably consistent with assumptions of random mating. We suspect our Indonesian subjects would disagree with this assessment, and we assure our own partners that we feel the same. Nevertheless, this scenario illustrates one of our key points: social scientists may exaggerate the consequences of choices made by individuals. Thus a pan-selectionist population model that assumed (evolutionary) selection in mate choice at the scale under study here would likely be wrong.

removed by drift. In the case of baby names, Hahn and Bentley found that the observed distribution is consistent with a neutral model, not selection.⁵ While any number of selectionist models could be proposed for the frequency distribution of baby names, there is only one neutral frequency distribution for any given data set and population model. This distribution depends solely on the total population size and the rate at which new names appear. If selection is present, it will cause departures from the neutral distribution that are readily detectable if the sample size is sufficiently large.⁶

We draw two conclusions from this example. First, baby names are an example of a cultural phenomenon that changes on a historical time scale, one that lends itself to a Darwinian evolutionary approach (namely, a population model of variation, inheritance, and differential rates of reproduction). Second, the neutral test shows this particular population cannot be distinguished from neutral expectation; that is, there is no evidence for it being under selection. This result does not imply that selection plays no role in the choice of baby names, but individual choices by parents do not produce a broader change in the population of names. This point again highlights a relevant ambiguity in the meaning of the word “selection”: parents certainly select names, but this may or may not lead to selection in a Darwinian sense.

To clarify the implications of this example, imagine that a researcher interested in baby names decided to skip the neutral test, and instead model the selection of names by creating an evolutionary game. This could take the form of a competition to pick the “best names” in each generation—perhaps names that are not too common in the population or those that carry a lot of prestige. Any number of games could be constructed in this way, but because the system is actually neutral, they would all be incorrect. This error would go undetected unless researchers shift their attention away from the selective advantages possessed by the “best” names to the full frequency distribution of names.

5. Strictly speaking, it is more accurate to say that the data do not reject neutrality. Under rare circumstances, distributions that are actually under selection might appear neutral—most commonly, where selection is only acting only very weakly. Furthermore, as with any statistical test, Type II (or β) errors will also occasionally be observed; that is, we might not reject the null hypothesis when it is actually false. Type II errors are closely related to the sensitivity of the test being used—something that should always be inferred.

6. Note that this does not preclude the possibility that selection has produced evolutionary change at other scales. Thus, a recent study by two sociologists (Lieberson and Bell 1992) found statistically significant differences in the choice of names among certain subpopulations, thereby suggesting that cultural notions about the naming of children may vary among smaller population groups. However, these subpopulations would need to be defined and some version of neutral testing applied to each of them to discover whether this variation in naming actually leads to departure from neutral expectation at the subpopulation level. In this particular instance, such a test was not done. Our point is that it is necessary to run some test for neutrality before devising a role for selection rather than a priori assuming that selection must be acting.

Type 2: Culture as It Affects Biological Evolution

Consider now type 2 cultural evolution, in which culture has some effect on biological fitness. Many studies in evolutionary social science fall into this category. For example, Winterhalder and Smith (1992:23) state that in evolutionary ecology, “analyses typically take the form of the following question: in what environmental circumstances are the costs and benefits of behavior X such that selection would favor its evolution?” Indeed, most research in human behavioral ecology is explicitly pan-selectionist, asking, “what are the fitness effects of different strategies in particular environments?” (Clarke and Low 2001:637) rather than “are the behaviors we observe actually under selection?”

In type 2 cultural evolution, culture can produce evolutionary change by giving some individuals a selective advantage. Two genetic methods have recently been developed to assess whether this actually occurs in human populations. Surprisingly, perhaps, neither method is based on a hunt for genes. Instead, both use noncoding regions of the genome as markers to assess changes in population genetic diversity. As we will see, such changes can be caused by either cultural or biological evolution.

One measure of Darwinian fitness is reproductive success: selective advantage may translate into more descendants. Genetic markers can be used to discover whether this has occurred in real populations by examining the distribution of genetic diversity. For example, we inherit our mitochondrial DNA only from our mothers (it is not subject to sexual recombination). Some noncoding parts of this molecule undergo rapid mutation; these are called hypervariable regions and can be used as markers to estimate the relatedness of individuals. Comparing any two people, the less variation in their hypervariable regions, the more closely they are related. At one extreme, individuals who share a very recent common female ancestor will carry the same mitochondrial haplotype (i.e., set of neutral mitochondrial DNA markers). An analogous approach can be used to identify haplotypes based on shared patrilineal descent, using noncoding regions on the nonrecombining portion of the paternally inherited Y chromosome (NRY).

Figure 1 shows how these genetic markers can help to evaluate the role of selection at the population level. If selection is not present (i.e., the system is neutral), every individual has an equal chance of producing offspring (fig. 1*a*). But if someone obtains a reproductive advantage, his or her descendants will become disproportionately abundant in the population (fig. 1*b*). There is also a third possibility: some individuals in each generation might attain higher fitness (i.e., have more children) but not pass this characteristic on to their own children. This produces a “Red Queen” dynamic, in which male dominance exists but seldom persists within families (fig. 1*c*). The Red Queen forestalls evolutionary change by preventing any descent group from gaining a lasting

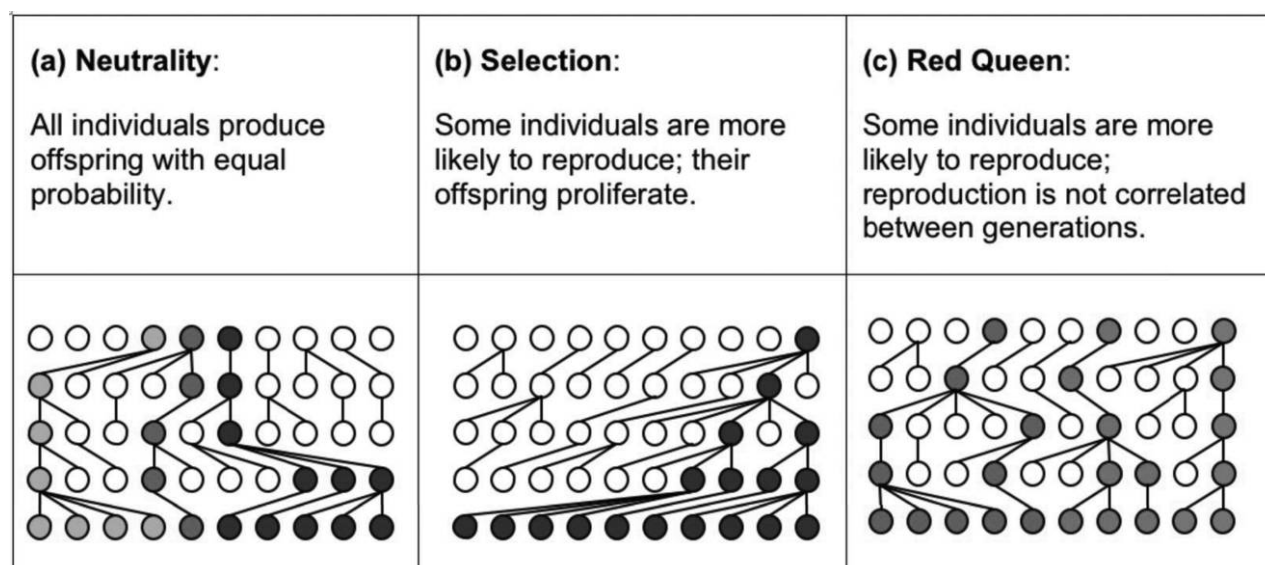


Figure 1. Noncoding genetic markers can be used to track lines of descent; here, each shade represents a single haplotype. Populations are at neutral equilibrium (a); undergoing selection (b); and experiencing Red Queen dynamics (c), in which dominance fluctuates and high fecundity is not inherited. A color version of this figure is available in the online edition of *Current Anthropology*.

advantage. As she explained to Alice, sometimes “it takes all the running you can do to keep in the same place.”⁷

All three processes—neutrality, selection with high heritability, and selection with Red Queen dynamics—generate distinctive patterns in the relative frequencies of haplotypes within populations. The first method developed to interpret these patterns was based on coalescent trees (Austerlitz, Kalydjieva, and Heyer 2003). These resemble the lineage diagrams long used by cultural anthropologists; both trace genealogies (“lines of descent”). Using haplotype data, a tree is constructed extending backward in time to the most recent common ancestor of a population sample. Because the haplotype mutation rate can be estimated, the time back to the most recent common ancestor (TMRCA) can also be inferred.

7. Originally proposed by Leigh van Valen (1973) and commonly conceptualized in the context of host-parasite arms races, the Red Queen hypothesis states that continuing adaptation is needed just to maintain fitness relative to coevolving systems. That is, in the context of an antagonistic coevolutionary arms race, evolution is occurring even though mean fitness remains nearly stationary. At its most simple, a Red Queen dynamic is simply the interaction between two (or more) competing evolutionary units. Here, we merely extend this definition to include different “families” (i.e., independent paternal lineages). The real significance of the Red Queen model is that it defines a particular form of evolutionary change that is measurably distinguishable from related models, such as simple directional selection or neutral drift. The nonheritable variation in male reproductive success described here results in reduced effective population size compared to neutral equilibrium but not as much as would occur as a result of simple dominance.

Both selective and demographic processes affect the branching patterns of these genealogies. Tree imbalance occurs if some branches become more or less bushy than predicted by a neutral demographic history. There are various statistical measures for computing imbalance for the whole tree, as well as measures for individual nodes. Generally speaking, tree imbalance shortens the TMRCA; or equivalently, it reduces the effective size of a population and, therefore, the amount of variation observed in the population. Using this method, Heyer and her collaborators discovered several cases of type 2 cultural evolution, in which culture has an effect on fertility, and hence, the overall direction of biological evolution (Heyer, Sibert, and Austerlitz 2005; fig. 2).

An interesting example comes from the Valserine Valley in France. Heyer (1993) showed that this population could be envisaged as two groups of families: first, stable families with a long history in the area who had relatively high reproductive success, and second, immigrants who had much lower (long-term) reproductive success. Although, in a superficial sense, historical immigration into the region was high, the “effective” immigration rate was actually relatively low due to the reduced reproductive success of immigrants.⁸ Over time, the core

8. “Effective” values are a necessary, if confusing, construct from evolutionary biology. Consider “effective” population size as opposed to “census” population size: not every individual alive today will contribute to future generations. Dying before you have children is evolutionarily equivalent to having not existed at all. Consequently, evolutionary ques-

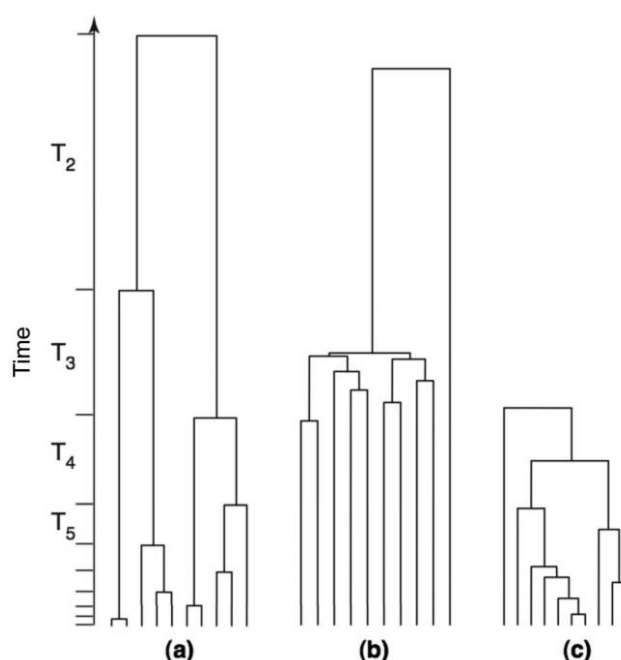


Figure 2. Example of coalescent trees. Typical genealogies are represented for a neutral population (a), strong selection just before the completion of a selective sweep (b), and cultural transmission of fitness (c). T_5 represents the length of time that the studied sample contains five genetic lineages; T_n therefore represents the time for n lineages. Adapted from Heyer, Sibert, and Austerlitz (2005).

group of stable individuals—the region’s “old families”—contributed more to future generations than the immigrants. From a biological perspective, this effect is nothing more than inbreeding among the old guard. Indeed, the social structure, transmitted from one generation to the next, has caused at least one genetic disorder to be maintained at increased frequency despite the superficially high level of gene inflow from surrounding populations. Nor is this example particularly unusual among human groups: exactly the same effect has been found elsewhere (Austerlitz and Heyer 1998). Such cultural pressure on biological evolution typically reduces the “effective” size of a population, and it is worth emphasizing that this will seldom be advantageous. As this example shows, type 2 cultural evolution, sometimes described as the cultural transmission of fitness, can counteract the effects of beneficial natural selection and will typically increase the frequency of disadvantageous alleles (e.g., disease genes or albinism).

The method of coalescent tree imbalance provides a

tions are usually more concerned with the number of individuals who contribute to future generations (i.e., the “effective” population size) rather than simply considering the number of individuals living in a population at any given moment.

straightforward way to discover departures from neutrality.⁹ As shown by Blum et al. (2006), 5 or 10 generations of cultural fertility transmission is enough to create an imbalance in the tree topology, and this effect can still be detected after ~20 generations (~50 in the strongest cases). We have recently developed another approach, which borrows from adaptations of the neutral theory by ecologists to explain the abundance of species in ecological communities. This method allows us to ask the same questions about the frequencies of haplotypes in human communities that Hahn and Bentley asked about baby names: are they consistent with selection or neutrality? The effects of selection are easy to detect: if a dominant lineage has high reproductive success, its haplotype will become more abundant at a rate proportional to its selective advantage. Thus, researchers have discovered that a Y chromosome haplotype, speculatively attributed to Genghis Khan, is very common in central Asia (Zerjal et al. 2003).

9. Note that we are not advocating for any particular test of neutrality. Hahn and Bentley used a variant based on power curves; Heyer and colleagues used a method based on imbalance in coalescent trees; our own research has largely employed a test based on Ewen’s sampling formula. We emphasize the need to test for neutrality before modeling selection, but we fully expect that different tests will have different power in different circumstances.

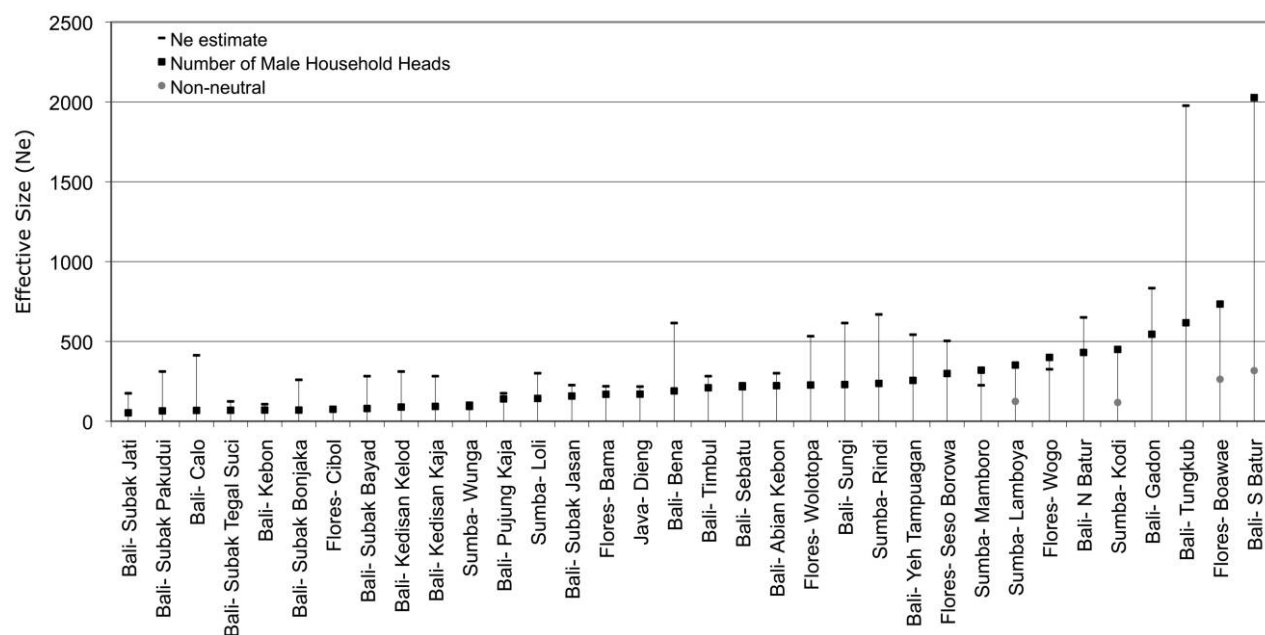


Figure 3. Estimates of effective male population size (N_e) for sampled communities together with known census sizes. Data are sorted by census size, and six sites for which census data were not available have been excluded. Dashes above squares indicate N_e estimates that are larger than census sizes; dashes below squares indicate a reduction in N_e . Gray circles indicate sites that tested as nonneutral. Of these five sites, four sites showed a reduction in N_e and one site lacked census data. The data point for South Batur indicating an effective male population size of $\sim 2,000$ is correct.

Human behavioral ecologists have long argued that we should expect to see evidence for selection in human communities due to the correlation between social dominance and fecundity: “In more than one hundred well studied societies, clear reproductive rewards for men are associated with status: high-ranking men have the right to more wives” (Clarke and Low 2001:637). However, evidence for this claim derives from demographic statistics collected over very short timescales (a few generations at most). Even if dominance is correlated with fertility over short timescales, a Red Queen effect could nullify any long-term evolutionary consequences. In that case, while some individuals might produce significantly more offspring than others, this tendency would not persist among their descendants.

Male Dominance and the Red Queen

If male dominance often translates into more descendants, this will be apparent from the distribution of NRY haplotypes in communities, as well as from their effective population sizes. We carried out this analysis for 41 Indonesian villages. These communities included neolocal Borneo hunter-gatherers and central Javanese rice farmers, matrilineal horticulturalists on Flores, patrilineal Balinese wet-rice farmers, and patrilineal horticultural clans on Sumba, Nias, and Flores.

Estimated effective and census population sizes (which, we emphasize, are quite different measures) are shown in figure 3.

To our surprise, we found that 88% of these communities (i.e., all but 5 of 41) are at neutral equilibrium with respect to the distribution of NRY haplotypes (for full methods, see Lansing et al. 2008). Figure 4 shows examples of both simulated and real haplotype frequency distributions. Neutral distributions exhibit considerable variation; examples of simulated neutral distributions in samples of 35 men drawn from populations of 100 and 300 are shown in figure 4a. To compare with real data, two typical neutral villages are shown in fig. 4b, and two nonneutral communities in fig. 4c. Three of the five nonneutral villages are consistent with positive selection (i.e., potentially male dominance), while the other two instead appear to be the result of recent demographic processes (i.e., rather than haplotypes being too similar, they actually appear to be too diverse).

The remaining 36 villages in the study were at neutral equilibrium. This does not imply that social dominance or competition between males does not occur in these communities,

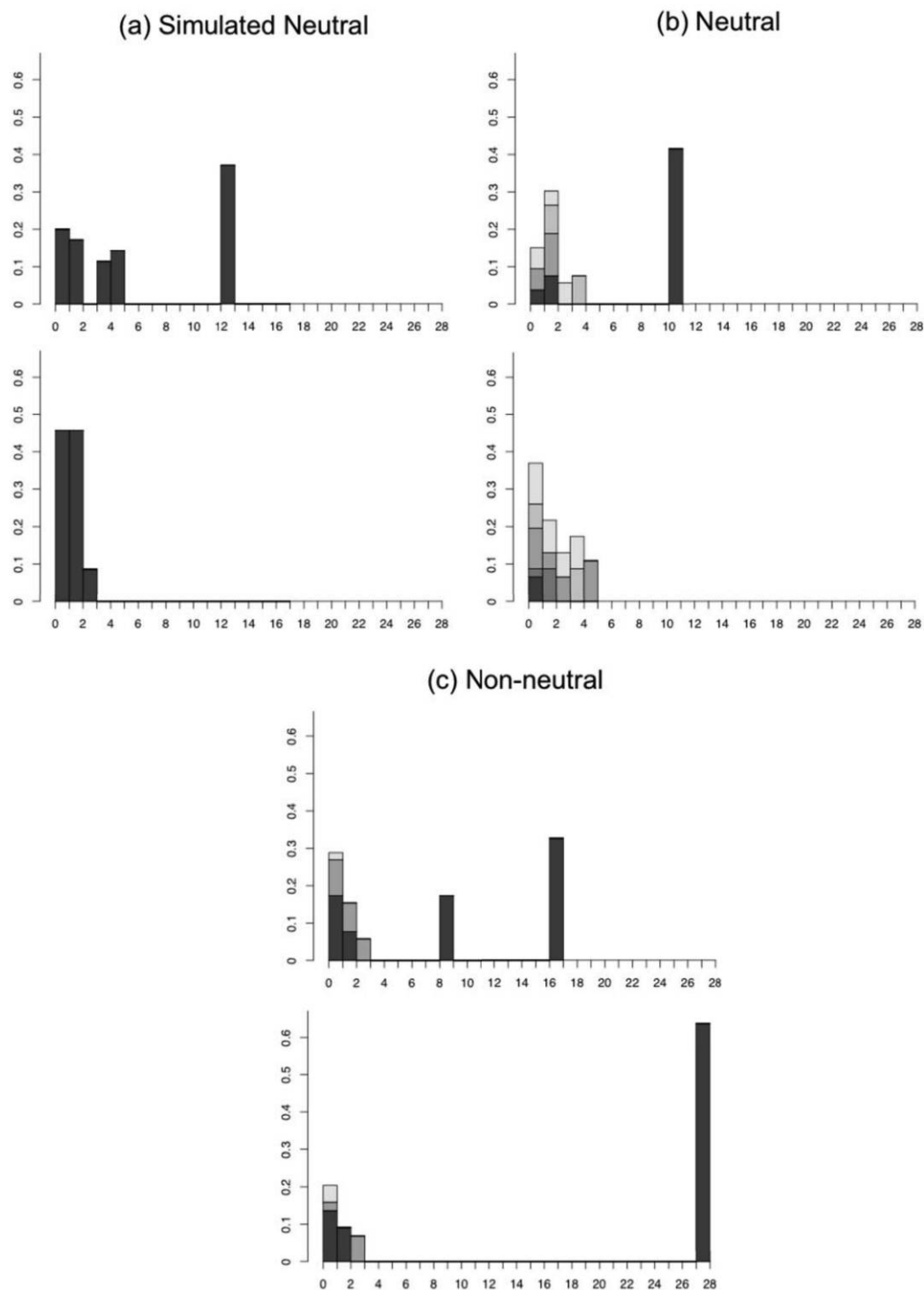


Figure 4. Nonrecombining Y chromosome (NRY) haplotype distributions. Frequencies are shown on the X-axis; number of carriers on the Y-axis. *a*, Simulated neutral data sets; *b*, *c*, observed neutral and non-neutral data sets, respectively. Grayscale shading in *b* and *c* identifies different NRY haplogroups. For example, in *b*, top, three different haplotypes—each from a different haplogroup—are represented by only a single carrier, whereas one haplotype is carried by 10 individuals (i.e., 40% of the population).

but it does mean that no heritable traits or behaviors that are passed paternally, be they biological or cultural, were under selection strong enough to have detectable evolutionary consequences. Interestingly, such deviations from neutrality persist for a long time. Figure 5 shows the return to neutrality from two extreme situations: all haplotypes initially identical

(lower curves in each panel) and all haplotypes initially different (upper curves in each panel). For an average-sized population (say, effective size $N_e = 400$), nonneutral diversity can be observed for ~ 20 generations, or ~ 600 years, following a selective event (for a male generation interval of 30 years; Fenner 2005). The finding that 88% of our Indonesian pop-

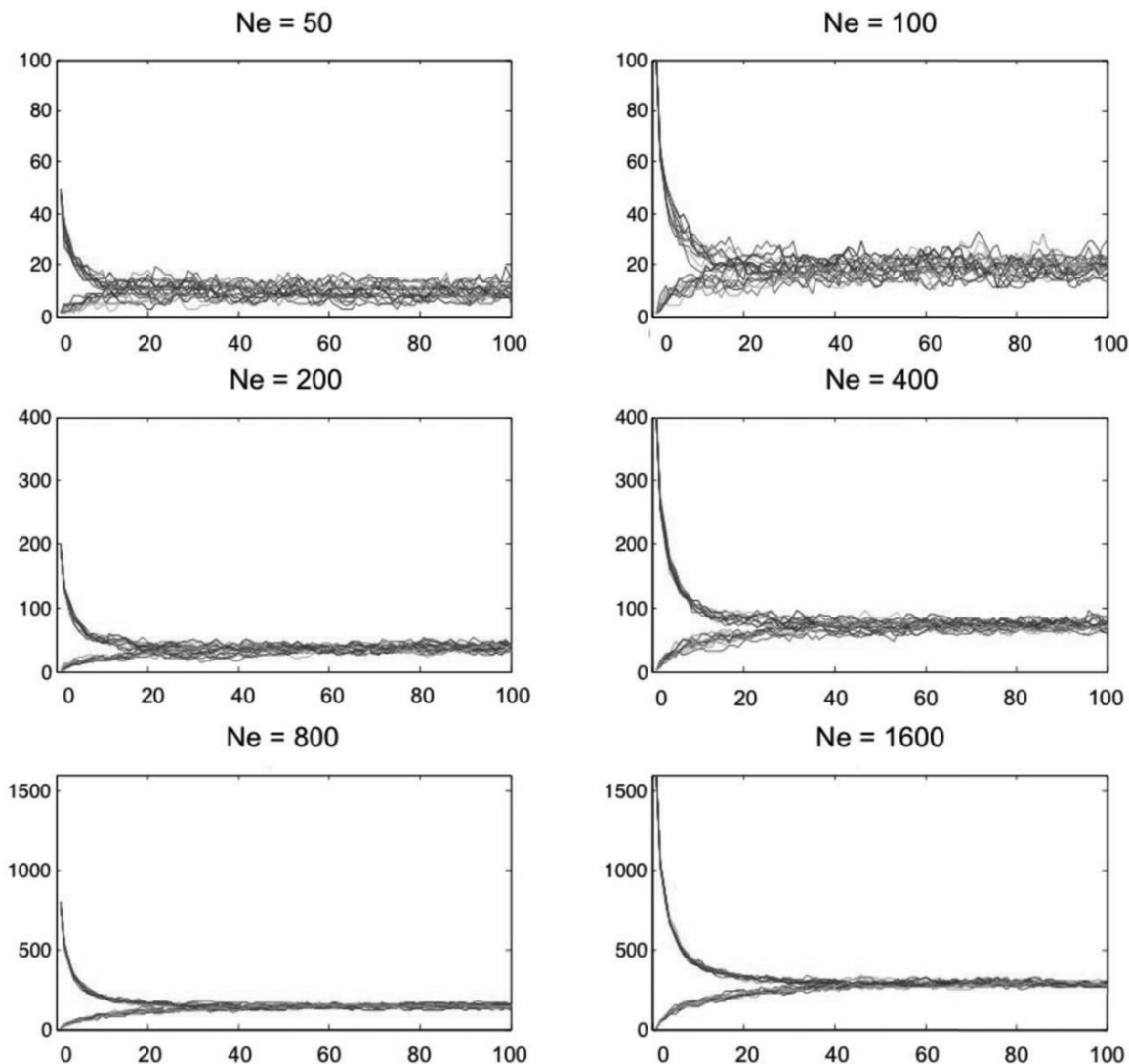


Figure 5. Persistence of nonneutral genetic diversity at different effective population sizes. Time in generations is shown on the X-axis; effective population size on the Y-axis. Initial conditions are extreme cases: either all unique haplotypes (upper curves) or all identical (lower curves). The mutation rate μ in these simulations is 0.0208, based on calculations for the Indonesian samples described in the text; and the male generation interval is 31 years (Fenner 2005). For an average-sized population ($N_e \approx 400$), nonneutral diversity can be observed for ~ 20 generations (~ 600 years) following a selective event. Therefore, we know that our neutral Indonesian populations have not experienced a detectable selective event for centuries. A color version of this figure is available in the online edition of *Current Anthropology*.

ulations exhibit neutral diversity is therefore doubly interesting. Not only are these populations neutral today, but they have also been undisturbed by selective events for a considerable period of time.

We draw two conclusions from these examples. First, in response to Lewontin, we have shown that the Darwinian model of heritable variation can yield insights into several different types of cultural evolution. Second, we saw that it is possible to test whether a given system is under selection, by looking for the signature of selection at the population level. No model of selection, including the replicators of evolutionary game theory, will be of use in understanding systems that are actually neutral. But if the system does show evidence of selection, what then?

Type 3: Coevolutionary Models

Humans, like beavers and termites, are vigorous practitioners of what biologists call “niche construction,” the active modification of their habitat, which can alter selection pressures on behavior through feedback relationships (Laland and Feldman 2000:132). Well-known examples for humans include the coevolution of animal domestication and adult tolerance to lactose in milk and the coevolution of sickle-cell anemia and malaria in response to increasingly settled communities (Durham 1991; Joy et al. 2003). These are examples of type 3 cultural evolution, the coevolution of culture and biology. Is a Darwinian approach well suited to model these kinds of interaction? If so, are evolutionary games the best approach?

Because they address the coupling of behavior with the environment, coevolutionary models often have lots of moving parts, which can easily obscure their inner workings. Hence it is preferable to choose toy examples that are as uncomplicated as possible. We begin with the simplest case, the interaction of one species with a single environmental parameter. The model is James Lovelock’s Daisyworld, in which natural selection is directly linked to environmental effects (Lenton and Lovelock 2000, 2001). We consider two variants of this model: neutral and coevolving.

Case 1: Neutral Daisyworld

This imaginary planet is a world like our own, except that it is mostly ocean.¹⁰ There is a chain of islands along the Equator, on which only daisies grow. The average temperature of Daisyworld is 22.5°C, and the daisies grow best at that temperature. The daisies are identical except for their color. As time progresses, different colored daisies appear by mutation, and their numbers fluctuate due to random drift. The resulting distribution of flowers on each island is in drift-mutation equilibrium.

10. This neutral version of Lovelock’s Daisyworld model is our own invention.

Case 2: Coevolving Daisyworld

Coevolving Daisyworld is identical to neutral Daisyworld except for two changes: (1) the ocean is replaced by land, and daisies can grow almost everywhere, and (2) the sun slowly grows hotter over time, much like our own sun.

These changes trigger a coevolutionary feedback process. Patches of dark flowers absorb more solar energy than light-colored flowers, making their local habitat slightly warmer. Consequently, when the sun is cool, the dark-colored daisies enjoy a selective advantage over light-colored flowers because the warmer temperature of the dark patches is slightly closer to the optimum for daisy growth. Conversely, when the sun grows hotter, the patches of light daisies are cooler. This difference in their microclimate gives them an advantage when the sun is hot, whereupon they outcompete the darker flowers.

This local fitness differential creates a feedback relationship at the global scale. It works like this: when the sun is cool, the dark daisies spread across the planet’s surface, and as they do so the warming effect also spreads. Eventually the entire planet is warmed to approximately the ideal temperature for the flowers, 22.5°C. Later on, as the sun grows hotter, the light daisies grow faster than black ones, replacing them and cooling the planet. Daisyworld’s temperature is thus maintained near the optimum for the daisies, despite changes in the sun’s radiance, as shown in figure 6.

Imagine that a team of astronauts arrives to study the flowers on both planets. What would they conclude? If they focus only on fitness differences between flowers, both systems will appear to be neutral. All daisies grow best at 22.5°C, and under these conditions, all flowers have the same fitness regardless of color. The only way to discover that coevolving Daisyworld is not neutral would be to apply a test of neutrality. This population-level comparison would show that color is under active selection on coevolving Daisyworld, but not on neutral Daisyworld, where the diversity of colored flowers is at neutral equilibrium.

A neutral test is enough to distinguish selection from neutrality, but importantly, it cannot explain why the two cases differ. While coevolving Daisyworld is under selection, an evolutionary game cannot explain the reason, because there is no fitness differential for the replicator equation to model; from the perspective of replicator dynamics, any environmental effects are considered only by proxy through the fitness of the daisies. This diverts our attention away from the real phenomenon of interest, the role of the flowers in planetary engineering. A full understanding of coevolution on Daisyworld requires a coevolutionary model, such as niche construction, which goes beyond variation in individual fitness to analyze the effects of environmental coupling at the population level (Lansing, Kremer, and Smuts 1998).

How important is this distinction? Suppose that our astronauts become interested in the economic potential of both planets as interstellar flower suppliers. On neutral Daisyworld, harvest techniques would not matter; while prolonged har-

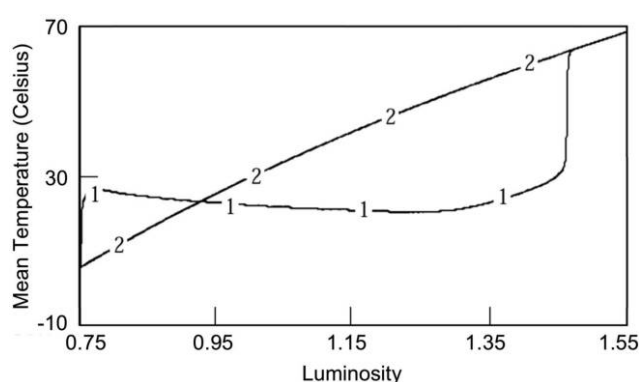


Figure 6. Simulated temperature regulation on Daisyworld. As the luminosity of its aging sun increases from 0.75 to 1.5 times the average value, the temperature of a bare planet would steadily rise (*line 2*). In contrast, the temperature of Daisyworld stabilizes close to 22.5° C with daisies present (*line 1*).

vesting might affect the daisies themselves, the environment would not be perturbed. However, on coevolving Daisyworld, there are two alternative possibilities. Selective flower harvests would cause tiny, probably unnoticeable tremors in planetary temperature. But clear-cutting large contiguous patches of daisies could cause global temperature regulation to suddenly fail.

Something very like this imaginary catastrophe occurred on the rice terraces of Bali. Because this case has been discussed extensively elsewhere (Lansing 2006, 2007), here we provide only a summary highlighting the parallel with the imaginary failure of temperature regulation on Daisyworld. In the 1970s, the Asian Development Bank became involved in an effort to boost rice production in Indonesia. The bank's consultants learned that on Bali, local groups of farmers synchronize their irrigation schedules. In most regions, these schedules produced two rice harvests of native Balinese rice per year. The consultants saw two ways to improve harvests. The first was to encourage the farmers to grow higher-yielding "Green Revolution" rice varieties, which produce more grain than Balinese rice. The second recommendation took advantage of another feature of the new rice: it grows faster than native rice. Consequently, the farmers could plant more frequently. The Ministry of Agriculture adopted both recommendations, and competitions were created to reward the farmers who produced the best harvests. By 1977, 70% of the southern Balinese "rice bowl" was planted with Green Revolution rice.

At first, rice harvests improved. But a year or two later, Balinese agricultural and irrigation workers began to report "chaos in water scheduling" and "explosions of pest populations." At the time, planners dismissed these occurrences as coincidence, and recommended higher doses of pesticides. However, a model of niche construction offers an alternative explanation for the harvest decline. On Daisyworld, the flow-

ers were coupled to a single environmental parameter—temperature. A niche construction model of Balinese farming requires two environmental parameters, water and pests—both of which are affected by a single strategic choice: the scheduling of irrigation. Traditionally, Balinese rice farmers manage their fields collectively in organizations called *subak*. Because irrigation depends on seasonal rainfall, each subak's choice of an irrigation schedule affects the availability of water for their neighbors downstream (fig. 7). The timing of irrigation can also be used to control rice pests like rats, insects, and insect-borne diseases. This is accomplished by synchronizing rice harvests and then briefly flooding the fields, thus depriving the pests of their habitat. The larger the area that is encompassed by the postharvest flooding, the fewer the pests. But if too many subaks try to flood their fields at the same time, there will not be enough water to go around.

To test the ability of the subaks to discover effective solutions to this trade-off between pest control and water shortages, we constructed a forward-in-time simulation model. Through a process of trial and error, each subak seeks to discover an irrigation schedule that minimizes losses both to pests and water shortages. In less than a decade, a patchwork of synchronized irrigation schedules comes into existence, which closely resembles the schedules observed on the ground. As this occurs, rice harvests improve because water shortages and pest damage are reduced for the entire watershed. When the key environmental parameters are stabilized, variation in harvests declines because these benefits spread across the entire system.

The key feature of both Daisyworld and the Balinese example is that they appear to be neutral from the perspective of evolutionary game theory, which focuses on variation in fitness at the level of individuals. Yet in reality, both are examples of tightly coupled coevolving systems. These phenom-

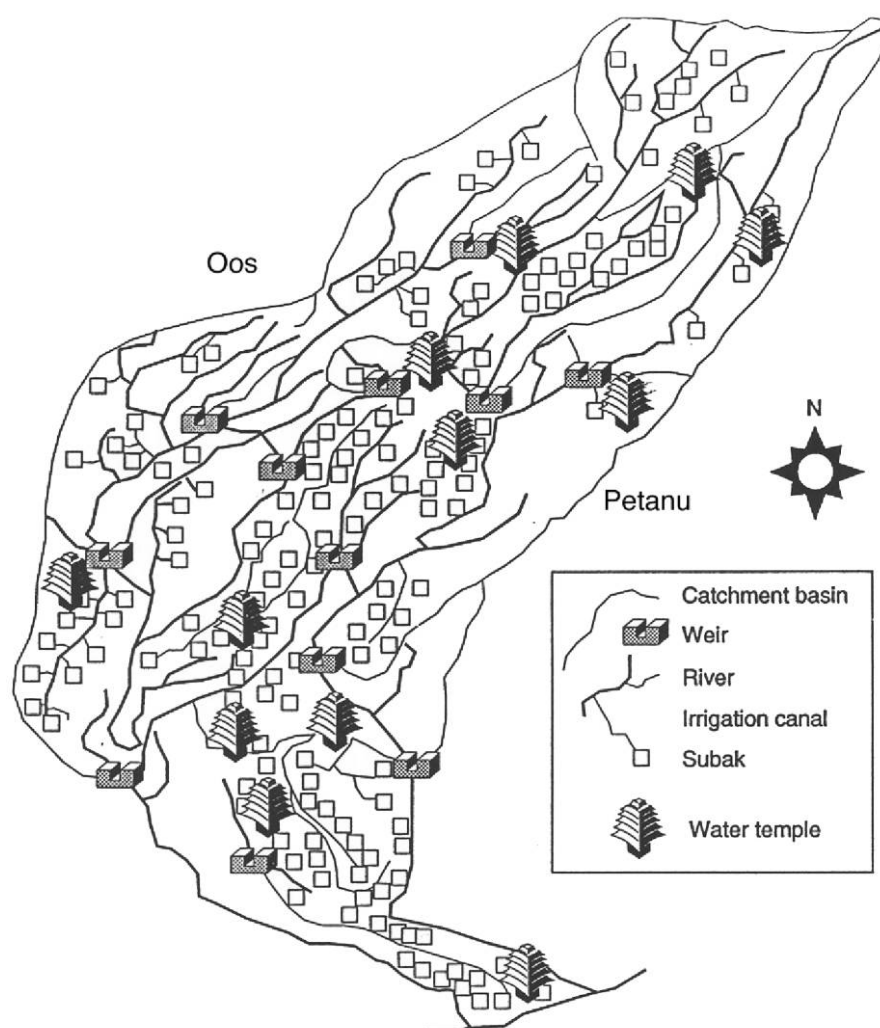


Figure 7. Subaks, rivers, and irrigation systems along the Oos and Petanu rivers of southern Bali. Traditionally, each subak is free to choose its own irrigation schedule. Crop losses due to pests or water shortages can be avoided by synchronizing irrigation with different-sized clusters of neighboring subaks. Map is not to scale, subaks are not rectangular, and many more water temples exist than are depicted here. From Lansing (2007: 119).

ena cannot be modeled with evolutionary games, to which they are effectively invisible.¹¹

Perhaps, then, it is relevant to note that when pests and water shortages destroyed harvests in Bali, consultants inter-

preted these problems as chance misfortunes. They urged the farmers to apply higher doses of pesticides while continuing to compete to grow as much rice per year as possible. This actually intensified both the pest problem (Machbub, Ludwig, and Gunaratnam 1988; Lansing et al. 2001) and water shortages (Horst 1998). It was only when farmers spontaneously returned to synchronized planting schemes that harvests began to recover—a point subsequently acknowledged by the evaluation team from the Asian Development Bank (Lansing 2007:124–125):

Substitution of the “high technology and bureaucratic” so-

11. Lansing and Miller (2005) constructed a two-player evolutionary game to model the trade-offs between water sharing and pest control. Unlike in standard evolutionary games, in this model the strategic payoffs depend on environmental parameters, which are affected by player's decisions about synchronized cropping. But this model does not permit coevolutionary feedback to occur. For that it is necessary to embed the simple two-player game within a larger, coevolutionary model (Lansing 2006).

lution in the event proved counter-productive, and was the major factor behind the yield and cropped area declines experienced between 1982 and 1985. . . . The cost of the lack of appreciation of the merits of the traditional regime has been high. Project experience highlights the fact that the irrigated rice terraces of Bali form a complex artificial ecosystem, which has been recognized locally over centuries. (Project Performance Audit Report, Bali Irrigation Project in Indonesia; Asian Development Bank 1988)

Conclusion: Short Hops on the Evolutionary Streetcar?

"The most important question," Lewontin recently wrote, "is why we should use a Darwinian model at all for history and culture" (2005: 23). Here we have described cases in which Darwinian models offer some insights into a range of cultural phenomena. However, these examples should give pause to the proponents of a pan-selectionist view of cultural evolution, the real target of Lewontin's critique. In standard evolutionary games, replicator dynamics drive an optimization process fueled by fitness differences, and the most successful phenotypes (i.e., strategies or players) become dominant. But in the examples we have considered, this did not occur. Instead, drift overwhelmed selection, effective population sizes decreased, the Red Queen suppressed fitness differences, and niche construction improved harvests. Modeling any of our systems as evolutionary games would fail to reveal these dynamics and thus divert attention from the models' most interesting features.

Consequently, we have emphasized the need to go beyond models of individual selection, to assess the consequences of selection at the population level. It may be that this point is even more important for anthropology than it is for genetics and ecology. Biologists have the luxury of thinking in terms of deep time, while cultural phenomena are generally more ephemeral. The concept of limitless time is vital to one of the principal arguments in favor of evolutionary games in biology, the "phenotypic gambit." According to this argument, genetics can be ignored if the aim is to discover an evolutionary strategy that is stable against genetic perturbation and is a presumptive target for selection (Marrow, Johnstone, and Hurst 1996). Such models have an advantage over those of traditional population genetics due to their relative mathematical simplicity: by ignoring many of the details of genetic inheritance, game theory has been able to provide significant insight into a number of important biological problems (e.g., the evolution of altruism and sex ratios). The respective roles of evolutionary game theory and genetics in biology have been likened to a streetcar, where the successive invasion and replacement of mutants cause movement from stop to stop. The details of short-term movement between temporary stops of the evolutionary streetcar are the domain of conventional population genetics theory (Hammerstein

2005; Marrow, Johnstone, and Hurst 1996). Evolutionary game theory is thus free to investigate whether the ultimate destination of the streetcar is an evolutionarily stable strategy.

Whether this approach makes sense for many cultural phenomena is an open question. It seems more likely that in most cases involving culture, time horizons will be short, the streetcar may not reach its destination, and disruptive Red Queen dynamics may be commonplace in competitive situations. But to find out, we need more empirical studies that attend to both individual competition and its population-level consequences. The potential significance of environmental effects, often beyond the control or awareness of individual agents, is also underlined by the examples of niche construction in *Daisyworld* and Bali. As these models show, the consequences of coevolution at the global scale can be a reduction in fitness differences and the false impression that these systems are not evolving. We suspect that the fashion for replicators and evolutionary games may have hindered anthropologists from recognizing similar cases elsewhere.

Acknowledgments

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Comments

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Is There a "Neutral Theory of Anthropology"?

Lansing and Cox open a welcome discussion of the potential for neutral models in anthropology—it has been almost 50 years since the original neutral models were applied to DNA sequences (e.g., Kimura 1968) and then later to biological phenotypes (e.g., Lande 1976) and cultural data (Cavalli-

Sforza and Feldman 1981; Neiman 1995). This long history of research is a gold mine for studies of culture evolution.

In engaging with it, we first need to be careful not to conflate Kimura's neutral theory with a generic neutral model. While Kimura developed much of the population genetics of neutral alleles, his neutral theory was a larger argument that most molecular changes really are neutral: that too much genetic variation exists within and between species for all of it to be selected.

In contrast to the neutral theory, choosing a neutral model (with a particular population history) as a null hypothesis merely implies that nonsignificant tests are consistent with neutrality. This can be quite specific; particular types of elements of the songs of chestnut-breasted warblers, for example, are consistent with the neutral model, whereas other elements are not (Byers, Belinsky, and Bentley 2010). What is more challenging is to demonstrate more than mere consistency with neutrality, as many selective models can give the same patterns of nucleotide variation as neutral models. For example, Gillespie (1977) showed that a straightforward model of balancing selection gives exactly the Ewens-Watterson distribution of allele frequencies promulgated by Lansing and Cox. In fact, for molecular evolution, recent genomic data no longer support the neutral theory or even neutral models as the null hypothesis (Hahn 2008).

What, then, justifies neutrality rather than selection as the null model? Parsimony can be one justification (e.g., Gould and Lewontin 1979), but a stronger justification would also include evidence that the process, not just the pattern, is consistent with the neutral model. In our study of baby names (Hahn and Bentley 2003), we deliberately chose a process involving discrete, tractable replicators (names), which are copied exactly from one person to another, except for the relatively rare (but persistent) invention of unique new names. We chose a unique time and place—twentieth-century United States society—in which first names could be copied relatively indiscriminately (to an unprecedented degree, compared to traditional kinship systems). Had we then “zoomed in” to smaller scales within the United States, we ought to have encountered a scale where the neutral model is falsified by discernible communities in which particular names are strongly selected (e.g., Fryer and Leavitt 2004; Smith and MacRaidl 2009). Archaeologists have used this to identify prehistoric communities, which come into focus at the scale where the neutral model is most strongly falsified (Lipo 2001).

For large societies, neutral models often seem more appropriate than approaches like repeated Prisoner's Dilemma games (RPDG), which often feature one-on-one contests with binary (e.g., cooperation vs. defection) options. In contrast, the real world is replete with complex, multiperson “games” involving multiple, possibly countless, different choices. Also, unlike RPDG experiments with viruses (Turner and Chao 1999), humans are usually too capricious, spontaneous, and imitative to adhere to the rules of the game (e.g., Traulsen et al. 2010). Instead, humans like to copy each other—it saves

time and is usually a safe bet. In a recent RPDG computer tournament, the winning strategy was one that regularly copied the successful strategies of others, with a bias towards discounting older information (Rendell et al. 2010).

In the internet age, the massive, highly replicative nature of modern online society means that the process of cultural transmission may be more like a neutral model than ever before. Copying others predominates in online behavior because copying hyperlinks is how the network is built, and exact copying is inherent to “friending” someone on Facebook, posting a link to news on a blog, or citing a paper that you have never read (e.g., Simkin and Roychowdhury 2003). Living and working online, people have perhaps never copied each other so profusely (since it usually costs nothing), so accurately, and so indiscriminately. The lack of discrimination applies not only at the aggregated population scale but even possibly (needs testing) at the individual scale. There is tremendous potential for testing both neutral and selection models of online behavior—never before have so many measurable data of human behavior been available, with new easily used tools such as Google Trends (cf. Bentley and Ormerod 2010).

Lansing and Cox give us several examples where neutral models fit cultural data quite well, but deciding whether a true “neutral theory of anthropology” exists still needs testing on many more data sets. Given the easy availability of online data sets that would have constituted a major research project just a decade ago, an avalanche of such analyses may already be on its way.

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Three general issues are raised in the review by Lansing and Cox (LC hereafter), as well as several particular points on which quantitative evolutionists may disagree. Both the general and particular issues have a much longer history than they imply.

The general issues can be summarized as three questions that I address sequentially. The first question follows from Lewontin's lectures at the Santa Fe Institute, “Is cultural evolution theory ‘based on Darwinian processes’ useful at all in light of Lewontin's claim that there are no cultural phenomena of ‘comparable concreteness’ to those studied in evolutionary biology?” Lewontin's claim, expanded greatly in Fracchia and Lewontin (1999), is that since there are no “units of culture” comparable to genes, inheritance and differential fitness of cultural units have no place in the study of culture change. Fracchia and Lewontin have two main reasons for this claim. The first is that culture is, by definition, a gestalt that cannot be broken down into parts that can be studied separately. The second is that for each culture, historical con-

tingency is much more important than such processes as transmission and/or selection.

I have addressed these (Feldman 2008) by an analogy with progress in biological science before and after the rediscovery of Mendel's rules of genetic inheritance. Before, biology was dominated by biometrics, and the whole biological phenotype was the accepted center of research, even for evolutionary studies. This led to errors in rules of correlation between relatives and almost no progress in the architecture of phenotypes until Fisher (1918) developed a plausible model of the relation between genotype and phenotype. The analogy with anthropology is that most of the field lies stuck in the quagmire of pre-Mendelian descriptive analysis, while the quantitative analysis of societal change is actively discouraged.

This is not to say that historical contingency is unimportant. Indeed it may be more important than deterministic processes for cultural evolution. But its importance can be quantified, as Sewall Wright did for biological evolution, in the extent of randomness relative to directional forces. In principle, Wright's random genetic drift and shifting balance theory can be incorporated into cultural evolutionary theory (Cavalli-Sforza and Feldman 1981), and indeed, they may be more important than the cultural differences in fertility and mortality discussed by LC.

The second issue raised by LC can be posed as, "Is evolutionary game theory the appropriate paradigm in which to articulate and model cultural evolution?" LC seem to claim that evolutionary game theory (EGT) and Darwinian models are equivalent, even to the extent that a rejection of a neutral model of cultural variation implies that this variation is a validation of EGT. Despite the claims of Nowak and Sigmund (2004) and Gintis (2006), EGT and Darwinian models are not the same, as has been pointed out elsewhere (Feldman, Otto, and Christiansen 1997; Spencer and Feldman 2005).

The difference between these is the difference between so-called adaptive dynamics and population genetic models of genotypic and phenotypic change. Adaptive dynamics (and EGT) make strong approximations about rules of genetic transmission (linkage is ignored, selection must be weak, and multiple stable equilibria, including polymorphisms, do not occur) and are based on the idea of evolutionary optimization. That is, phenotypes, such as behaviors, change in such a way that some function of the frequencies of these traits is optimized. The population genetic approach makes no such assumptions and, importantly, does not assume that local dynamics are sufficient to describe global dynamics. In the case of cultural evolution, where some modes of transmission among members of the population may be difficult to distinguish from a fitness advantage to the transmitted traits, EGT has even less of a role to play. In this case there may be conflicts between frequency change due to transmission and frequency change due to Darwinian processes; hence the possibility that maladaptive variants of a cultural trait may spread (Cavalli-Sforza and Feldman 1981; Lehmann and Feldman 2009). In fact the implication that evolutionary games and

replicator dynamics are the same, and that both "drive an optimization process," is incorrect.

The third question raised by LC is, "Is the selection neutrality debate relevant or approachable when the traits under study are cultural?" Here, I do not agree with LC that "there is only one neutral frequency distribution for any given data set and population model." The test of neutrality that has been borrowed from population genetics for use in ecology and archaeology is of the Ewens-Watterson form (Ewens 2004), and it assumes a particular form of mutation called the "infinite alleles model." Is this "the correct" neutral model for testing frequency distributions of cultural variants? The neutral distribution for babies' names, tested by Hahn and Bentley (2003), depends on this mutation model and it being the same in all segments of the population. Further, cultural and Darwinian selection may differ in their expected trait-frequency spectra. Thus neutrality is not unique, and not as simple as it seems.

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In this paper, J. S. Lansing and Murray Cox broaden the classical view on cultural evolution in a Darwinian context too frequently restricted to an evolutionary game theory approach and consider three versions of this idea: purely cultural evolution, culture as it affects biological evolution, and gene-culture coevolution.

My first comment is on methodological difficulty for detecting transmission of cultural behavior linked to fitness (their version 2) with genetic data. I feel the authors do not stress enough all the methodological difficulties. One way to test for the existence of any transmission of cultural behavior linked to fitness is to study the distribution of genetic alleles in the population under study. When a such phenomenon exists, the distribution of genetic diversity will show in most of the cases a departure from neutrality. Indeed, in some cases two phenomena can coexist whose signatures on the human genome can counterbalance each other. For example, in the Quebec population, the demographic growth of the population changes the distribution of haplotypes in one direction, and the fertility transmission puts it back in the reverse direction, so that at the end the allele distribution is much closer to a neutral Ewens distribution than are distributions in the European source populations (Heyer, Austerlitz, and Labuda 2001; Moreau et al. 2009). Fortunately, other population genetic tests show the nonneutral pattern. Therefore, as the authors state it, neutrality should be tested first but not with only one test.

Once you have shown that your process is "nonneutral,"

the theoretical challenge is to decipher which evolutionary forces are involved: it could be biological selection, population growth, or cultural transmission of behavior. Classical population genetic studies have developed several tools to distinguish selection from population growth. But what remains even more difficult from a theoretical point of view is to distinguish between population growth and cultural transmission of a trait that is linked to fertility. Like population growth, cultural transmission of fertility has an impact on the whole genome. Thus, for most of the population genetics statistics, it will give the same results: effective size (N_e) is reduced, and coalescent trees are star shaped (Sibert, Austerlitz, and Heyer 2002). It was really a theoretical challenge to be able to design a statistical test that can untangle population growth from fertility transmission. Thanks to the help of several mathematicians we have designed one that is based on the imbalanced shape of coalescent tree (Blum et al. 2006). Until now these tests have been used only on uniparental markers, and a new challenge is to extend their application to autosomal markers. Indeed, when fertility transmission is detected on uniparental markers, we cannot rule out the possibility that biological selection is the driving force. If the same signal is detected on several independent markers (i.e., autosomal) this strengthens the conclusion that fitness-linked behaviors are culturally transmitted. Not until such tests are designed will we be able to evaluate properly the importance of the cultural transmission of behaviors linked to fitness in different cultural and geographical areas.

My second comment is about an aspect of cultural transmission that is not emphasized enough by the two authors, the fact that cultural transmission is far from efficient. This is a key issue for evolutionary game theory approach. In most evolutionary game theory, it is frequently assumed that the most successful strategy or cultural trait will become the most frequent. From our knowledge, this is far from obvious because of this inaccuracy in transmission for cultural traits. In the Quebec population (Austerlitz and Heyer 1998), large families tend to have children who will have large families on their own, but the "large family" phenotype does not invade the population. Indeed, there is a high probability for a "large family" to become a "small family" in the next generation, that is, to "mutate." The process is then equivalent to a selection/mutation model that reaches equilibrium. If you have a mutation rate high enough, the large family does not invade. In some cases it can go as far as erasing any signal, an extreme case that Lansing and Cox call the Red Queen evolution.

In my view it is quite likely that the cultural transmission will be much less efficient than genetic transmission, that is, that a high "mutation rate" will be seen in the evolutionary trajectory.

My last comment is to broaden again the field of cultural and biological evolution. I want to emphasize that culture has an impact on our evolution not only through selective processes such as gene-culture coevolution but also through neutral evolution. The most classical examples are the importance

of cultural barriers to mating, as in the cases where language or religion create a limitation of gene flow. This has an important role in shaping interpopulation genetic diversity. Furthermore, cultural behaviors can also shape the intrapopulation genetic diversity by reducing effective population size through social organization (Chaix et al. 2007; Ségurel et al. 2008). In conclusion, the vast field of interactions between culture and genetic evolution in our species is a promising research area, and I agree with Lansing and Cox that it is far from limited to evolutionary game theory approach.

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I found this is a frustrating article. It begins with an abstract that makes various strong claims, some of which are barely addressed in the article. The authors raise a variety of provocative issues—Lewontin's dismissal of cultural evolutionism, the centrality of game theory in evolutionary analysis, distinguishing selection from neutrality—that are never sufficiently explored nor clearly linked. The paper is less than the sum of its parts, and some of the parts are quite problematic. Nevertheless, Lansing and Cox do introduce CA readers to some important debates, though not in the most enlightening fashion.

According to the abstract, "the relevance of EGT [evolutionary game theory] depends on whether its assumptions are met. Those assumptions are quite restrictive: selection is constant, time horizons are deep, the external environment is not part of the game, and neutral processes such as drift are irrelevant." These are strong claims, and I find them overstated at best. Like many theoretical models or abstractions, EGT can be "relevant" in the sense of explaining a substantial amount even when its assumptions are not strictly met. Furthermore, most of the assumptions listed are not really central to EGT; "constant" selection, for one, is explicitly not assumed in the large and well-studied class of games where payoffs (selection coefficients) vary according to the population frequency of different strategies (e.g., hawk-dove). Many current applications of EGT recognize the important role of stochastic factors such as mutation and drift and often explicitly incorporate those into simulations structured around EGT models. Models of cultural evolution, such as those developed by Boyd and Richerson (1985, 2005), typically incorporate specific parameters involving neutral or stochastic factors, such as error (e.g., in copying), sampling (e.g., of cultural models by naive individuals), and the like. The well-known result that two or more strategies may have equal payoffs in specific game environments, and therefore can invade via drift, plays an important role in many EGT models of the evolution of cooperation. The abstract's concluding claim,

that “exclusive reliance on EGT can obscure the respective roles of selective and neutral processes,” may well be true, but I question how many evolutionists who rely on EGT actually do so “exclusively.”

The article is pervaded with affirmations of null models (“neutrality”) when what the analyses cited actually demonstrate is failure to reject a null model. This misrepresentation of elementary statistical logic is especially troubling because the authors are aware of it but acknowledge the point only in a footnote. This seems part of a larger pattern of promoting skepticism concerning the importance of natural selection and adaptation in biology and anthropology. Thus, the classic attacks of Gould and Lewontin are repeatedly cited, but the (to my mind definitive) rebuttals of same are ignored (e.g., Alcock 2001; Maynard Smith 1978; Mayr 1983; Queller 1995); a quotation from Kimura (1983) is deployed to suggest that selectionist explanations routinely rely on facile stories rather than quantitative evidence; the burgeoning evidence for rapid and pervasive natural selection on the human genome goes uncited; and so on.

Lansing and Cox represent the logic of adaptationist research in sometimes simplistic ways. Consider their analysis of paternal lineages in Indonesia. Finding that most populations do not exhibit differential long-term success in any given Y-chromosome haplotype, they conclude that short-term correlations between social dominance and fecundity have no long-term evolutionary effects. But all these results show is that social dominance in these populations is not linked to genes on the nonrecombining segment of the Y chromosome. In any case, any genetic variation for reproductive dominance would quickly be exhausted by selection (the genes coding for dominance going to fixation). Instead of selection for dominance per se, a more plausible scenario (one that actually invokes EGT) involves a heritable conditional strategy: if one happens to have a phenotype that is endowed (by inheritance or circumstance) with features that allow one to gain social dominance and thereby relative reproductive success, seize the opportunity. Such a strategy, transmitted culturally or genetically, could go to fixation and be maintained by selection and yet still be consistent with apparent neutrality of Y-haplotypes. In contrast, the simple neutrality argument apparently advocated by Lansing and Cox implies that all the phenomena associated with social and reproductive dominance (phenomena that are ubiquitous in vertebrates, including our primate relatives) are just noise—sound and fury signifying nothing.

On a positive note, the short section on evolutionary feedback and niche construction leads in a useful direction. Evolutionary analyses definitely need to investigate these kinds of processes in order to gain further insight into cultural and behavioral phenomena. I am not nearly as skeptical as Lansing and Cox that EGT has nothing to offer in this regard, but it is perhaps too early to tell.

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Lansing and Cox note that it is easy to look at a phenomenon or a set of empirical patterns and develop post hoc adaptive or selective explanations. This fact has been widely discussed within evolutionary biology, and this discussion is responsible for the centrality of “tests of neutrality” within the field. Lansing and Cox argue convincingly for an increased role for formal tests of neutrality in the analysis of cultural data. We wish to raise a related issue that is less well understood in the biological evolution community but that we believe underlies many of its most persistent controversies.

Whether or not a particular analysis provides support for the action of natural selection depends in no small part on the grain of analysis and the scope of the alternatives considered by the modeling framework used. Lansing and Cox, like many writers in evolutionary biology, treat models based on adaptation and models based on other population genetic factors as rivals: in their application to a particular case, they are treated alternative explanations of the same phenomena. However, we think that in both the biological and cultural cases, this is not quite the right way to think of the relation between adaptationist and population-genetic models. We suggest, instead, that good adaptive explanations tend to be at a slightly coarser grain of analysis than population-genetic models. Different tools consider different timescales of evolution and, implicitly, different sets of alternatives.

A good way to think about this is with the metaphor of an “adaptive landscape” (see Wilkins and Godfrey-Smith 2009). In this metaphor, we imagine a large set of alternative types represented in a space, where the “height” in this space reflects the relative fitness associated with those types. An adaptive process, if one is present, takes the population from valleys to peaks. Other processes may produce change in a way that does not track fitness. Population-genetic tools, which consider changes in allele frequencies over the course of generations, focus attention on a narrow region in the space of all possible genotypes or phenotypes, all closely related to the type(s) observed in the data. Analyses at this scale tend to emphasize the importance of mechanistic constraints (such as recombination) and random sampling (genetic drift). Natural selection when seen at this scale is one factor among many, and it has limited predictive importance. Game-theoretic tools, by contrast, tend to consider somewhat longer timescales, and a larger set of alternatives. They are concerned not with the fine details of movement on the landscape but with a general and longer-term tendency for the population to spend its time near peaks rather than valleys. In this sense, an adaptationist model is more “zoomed out” than a population-genetic one. The analyses invoked by paleontologists

and in studies of the evolution of development tend to zoom out even farther, considering observed forms in contrast to a broad range of hypothetical alternative types. At this coarsest grain of analysis, selection again recedes in perceived importance, as the large set of conceivable alternatives highlights the great importance of historical contingency in producing observed forms.

We suggest that a similar set of issues is expected to arise in the context of analyses of cultural evolution. The exact relations between population-genetic factors and adaptation seen in biology will not be identical to those in the cultural context, but a similar set of relationships between subtly different levels of “zoom” may be found. One kind of model looks at the fine structure of change in a population, with an important role for the quirks of transmission rules and random sampling, while another kind of model might look at coarser-grained patterns in the process of cultural change, by which cultures tend to adapt to environmental conditions and reach game-theoretic equilibria. If selectionist thinking has a role in explaining cultural change, we suggest it will be at an “intermediate level of zoom” in a way analogous to the biological case.

It is common for ideas central to our understanding of biological evolution to be invoked in the interpretation of patterns in cultural data. Lansing and Cox have made a compelling argument for approaching the analysis of cultural evolution with objectivity and rigor, to avoid an explosion of “just-so stories.” We applaud their argument and simply add that the rigorous application of statistical models should be coupled to an equally rigorous consideration of the assumptions and contrasts that implicitly “frame” the content of those models.

Reply

Many of the reviewers’ comments are concerned with population genetics. Because *Current Anthropology* is not a genetics journal, we think it may be helpful to summarize some background for readers who are not biologists.

Before the 1960s, most genetic variation—ultimately encoded by changes in our DNA—was thought to be maintained by Darwinian selection. However, as knowledge of the human genome accumulated, it soon became clear that we harbor too much genetic variation for most of it to be under selection. This proposition—that the majority of genetic variants are neither good for us nor bad—came to be known as neutral theory. It is now recognized that DNA can be divided into two types: genes, which may be affected by Darwinian selection, and noncoding regions, which selection cannot see and therefore cannot affect. However, these noncoding regions are very useful for studying history. For example, by examining the accumulated variation in noncoding regions of the Y chro-

mosome, geneticists can infer common ancestry: comparing two men, the more similar their noncoding sequences, the closer their patrilineal relatedness.

With this background, we turn to Eric Smith’s remarks. Smith takes issue with one of our examples, a study of the evidence for male dominance in 41 Indonesian villages (Lansing et al. 2008). In this analysis, we used neutral genetic markers to identify groups of patrilineally related men. We then asked whether, in each village, the frequency distribution of patrilineal groups (how many patrilineal groups and how many men in each) could be produced by chance alone. Alternatively, the distribution of patrilineal groups could have been skewed by demographic processes, such as an influx of newcomers, or by male dominance: one or a few dominant patrilineal groups outbreeding others. We found that in 88% of the villages, the distribution of patrilineal groups was consistent with neutrality, not only today but for many generations in the past.

Smith objects that “all these results show is that social dominance in these populations is not linked to genes on the nonrecombining segment of the Y chromosome.” If the reader has followed the discussion so far, it should be clear that this is a misunderstanding. We did not study genes. Indeed, we doubt that genes “for” dominance exist. We used neutral genetic markers on the Y chromosome merely to identify shared patrilineal descent. The cause of variation in the distribution of these patrilineal groups within villages has nothing to do with “genes coding for dominance” on the Y chromosome. Instead, it reflects the past demographic history of each village. Over the past 10 or 20 generations, did some men achieve reproductive dominance and pass it on to their offspring?

We used the Ewens-Watterson equation to calculate the neutral distribution of patrilineal groups for each village. This equation assumes that population size is constant, and that the likelihood of having children is the same for all individuals in the population. As Feldman, Heyer, Bentley, and Hahn comment, while the Ewens equation is quite common in biology, there are other ways to test for neutrality. Two points are relevant here. First, the general reader may not appreciate that for any given parameterization of a demographic model, there is only one unique neutral frequency distribution. The Ewens equation is powerful because it makes precise predictions based on simple demographic assumptions: constant population size and equal probability that any individual will reproduce. For this reason, versions of this equation are widely used in both genetics and ecology. However, as Heyer, Hahn, and Bentley note, frequency distributions that look neutral can also be produced by balancing selection. This leads to the second point, appropriately stressed by several reviewers: while for any given demographic model there is only one neutral distribution, test results indicating that frequency distributions (or phylogenies) are consistent with neutrality need to be followed up by considering alternative explanations.

In our study of patrilineal groups in Indonesian villages, we did this by using a power analysis to detect departures from neutrality under varying demographic conditions (founder ef-

fects, bottlenecks, migration) and used additional parameters to characterize the reproductive consequences of male dominance. Our “Red Queen” model explored a scenario resembling balancing selection, in the context of reproductive competition. We simulated populations experiencing varying levels of male dominance and/or demographic change, sampled them 10,000 times, calculated the Ewens-Watterson equation for each replicate, and applied Slatkin’s exact test to observe departures from the expectation under neutrality. Our power analysis showed that even relatively short-lived episodes of dominance are detectable for tens of generations. In general, neutral changes in the composition of populations are Markov models, which eventually converge on an equilibrium distribution. If a community is evolving neutrally and the frequency distribution of individuals has not yet reached equilibrium, then the current population will retain some signature from the past. Consequently, cultural selection (or its absence) will leave a signal in noncoding DNA that can persist for centuries.

Although we did not suggest that the Ewens-Watterson equation is the best (or sole) framework for the analysis of cultural variants, several reviewers apparently took this to be our argument. We make no such suggestion; it merely happens that several of the models we discussed are based on the Ewens-Watterson equation, so we tried to explain how it works. In ecology, this test is beginning to be supplemented by other approaches (e.g., Etienne and Olff 2004), and we expect that new tests for neutrality will continue to appear. The tree imbalance method described by Heyer offers a different mathematical perspective on neutrality, and it has been successfully applied to language evolution by other researchers (Pagel 2009). In our view, the key point is that these tests differ from analyses deriving from replicator models in that they shift the analytical focus from the fitness of individuals to the population-level consequences of both evolutionary and stochastic processes. Any process that can be modeled using replicators will leave a signature in the population that can be tested for neutrality. Further, as our Indonesian example shows, population-level analysis using models developed for the study of neutral processes in biology offer a surprisingly rich perspective on the past. This population-based historical perspective is notably absent from replicator models.

Turning to other issues raised by the reviewers, Feldman states that the implication that evolutionary games and replicator dynamics are the same, and both “drive an optimization process,” is incorrect. We are puzzled by this comment. In his recent textbook, Martin Nowak describes the replicator as the “cornerstone of evolutionary game dynamics” (2006: 56); similarly, Hofbauer and Sigmund placed the replicator equation at the center of their 1988 textbook. The replicator equation descends from Fisher’s selection equation and certainly drives an optimization process. However, we think that Feldman nicely captures the key difference between population genetics and replicator models (“adaptive dynamics”) by

noting that replicator models assume that local dynamics are sufficient to account for global dynamics. This is a key premise that we hold to be false.

This leads us to the simple and elegant perspective offered by Wilkins and Godfrey-Smith. As they point out, different analytical tools are relevant to different evolutionary timescales. In genetics, mutations in genes produce variation in genotypes and phenotypes that can be exploited by natural selection. At fine scales of space and time, these variations cluster in small regions of the adaptive landscape. As the timescale increases, more mutations occur and selection has more material to work with. The “phenotypic gambit” justifies game-theoretical approaches at these scales: given enough time, mutations should produce enough variation for selection to find its way to optimal solutions.

It is worth noting, however, that the sources of genetic variation are well-understood chemical processes. Since the 1960s, geneticists have worked hard to quantify patterns of mutation in different parts of the genome and have found that, in noncoding regions, they are largely predictable. Selection is thus detectable as a departure from neutrality: selected regions of the genome change in different ways compared to neutral regions. These discoveries revolutionized evolutionary biology. The question is, are there analogous types of mutation in cultural phenomena? The best candidates are probably changes in some aspects of language (lexicon, phonology) and material culture. The regularity of lexical change enables researchers to infer historical processes from variation in the branch lengths of language phylogenies because words vary systematically in their rate of retention (Gray, Drummond, and Greenhill 2009). Similarly, in the last 10 years, archaeologists have used phylogenetic methods to infer population history from artifact distributions (Collard and Shennan 2008). However, as we note, biologists have the luxury of thinking in terms of vast evolutionary timescales. Whether cultural phenomena evolve to such optima or are instead relentlessly dominated by transient dynamics remains an open question.

Finally, we note that none of our reviewers commented on our discussion of coevolutionary models. We believe that understanding such systems, from the global scale (climate change) to the local (the commons), may be the key anthropological challenge of our time (Kendal, Tehrani, and Odling-Smee, forthcoming).

—J. Stephen Lansing and Murray P. Cox

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